

# Mercury exposure and survival in free-living tree swallows (*Tachycineta bicolor*)

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**Abstract** Mercury has become a ubiquitous contaminant in food chains worldwide. A large body of literature detailing bioaccumulation and effects on birds has revealed the potential for mercury to adversely impact avian physiology and reproduction. However, the extent to which these effects impair survival remains poorly understood. The objective of this study was to determine whether mercury exposure was associated with reduced annual survivorship in tree swallows (*Tachycineta bicolor*) breeding at a site with legacy industrial contamination. From 2005 to 2008, we captured and marked 932 adult swallows. We used Cormack-Jolly-Seber models and an information-theoretic approach to test our hypotheses that adult survival varied by sex, breeding location, and cumulative individual mercury exposure. Blood mercury was significantly elevated on contaminated sites (2005–2007 combined mean  $\pm$  SE:  $2.84 \pm 0.09 \mu\text{g/g}$ ; reference:  $0.17 \pm 0.01 \mu\text{g/g}$ ). Model-averaged estimates of female apparent survival ranged from 0.483 to 0.488 on reference sites and 0.473 to 0.477 on contaminated sites. For males, apparent survival ranged from 0.451 to 0.457 on reference sites and 0.444 to 0.448 on contaminated sites. Thus, we observed approximately a 1% difference in survival between mercury-contaminated and reference sites. Such a small difference is unlikely to impact population viability in this short-lived species; however, some songbirds accumulate mercury to a greater degree than tree swallows and do not possess the migratory behavior that removes swallows to less contaminated areas for the

majority of the year. Identifying whether such species are at risk of suffering biologically significant reductions in survival should become a focus of future research.

**Keywords** Heavy metal · Mercury · Survival · *Tachycineta bicolor* · Tree swallow

## Introduction

Mercury is a heavy metal that has contaminated countless ecosystems throughout the world (UNEP 2002). In its methylated form, mercury accumulates in animal tissue and concentrates at the top of food webs. Because methylation processes are largely restricted to aquatic environments (Wiener et al. 2003), piscivorous birds have long been considered most at risk of exposure and adverse effects (Wolfe et al. 1998; Scheuhammer et al. 2007). However, recent studies have concluded that both atmospheric and aquatic mercury can accumulate in non-piscivorous birds, including songbirds, with no direct link to mercury point sources (Rimmer et al. 2005; Shriner et al. 2006; Cristol et al. 2008).

While dosing studies on captive aquatic birds long ago established that mercury accumulation can affect avian survival and reproduction (e.g. Heinz and Locke 1976; Heinz 1979; Hoffman and Moore 1979), the extent to which such effects may occur in free-living populations remains unclear. Evidence is now mounting for individual fitness effects among free-living songbirds, particularly with regard to endocrine and immune physiology (Franceschini et al. 2009; Hawley et al. 2009; Wada et al. 2009). For example, Hawley et al. (2009) observed a reduction in humoral immune response among female tree swallows (*Tachycineta bicolor*) breeding at a contaminated site in Virginia, USA.

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Similarly, Wada et al. (2009) noted abnormal expression patterns for both corticosterone and thyroid hormone in contaminated tree swallow nestlings at the same location. Such physiological pathways directly underlie many of the processes important for reproduction, providing an abundance of potential mechanisms through which mercury might impact reproductive success. In fact, some progress has been made in identifying reproductive effects of mercury exposure in free-living birds (tree swallows: Brasso and Cristol 2008; common loons (*Gavia immer*): Evers et al. 2008).

Interruption of these same physiological pathways might also result in higher mortality among contaminated birds. However, evaluating the impact of mercury on survival is difficult because large, long-term data sets are required to produce accurate estimates. Additionally, many environmental variables likely influence survival in free-living populations, confounding analyses and making interpretation of results difficult. As a result, few attempts have been made to evaluate the impact of mercury on avian survivorship (Seewagen 2010). Thompson et al. (1991) found no effect of mercury on the return rate of great skuas (*Catharacta skua*) to their breeding colony in the following year. Likewise, Meyer et al. (1998) reported no relationship between mercury level and inter-annual survival in breeding common loons, a result that was later corroborated by a longer-term mark-recapture study (Mitro et al. 2008). To our knowledge, there exist no published studies examining the effect of mercury on annual adult survival in a free-living songbird population.

The objective of this study was to determine whether mercury exposure was associated with reduced survivorship in tree swallows breeding at a site with legacy industrial point source contamination. We used four years of mark-recapture data to test our hypotheses that (1) adult survival varied by sex, (2) adult survival varied by breeding site type (contaminated or reference), and (3) adult survival was related to cumulative individual mercury exposure.

## Methods

### Study species

The tree swallow is an insectivorous, migratory songbird that breeds throughout much of North America (Robertson et al. 1992). Tree swallows consume a diet that is both terrestrial and aquatic in origin (Robertson et al. 1992; Mengelkoch et al. 2004; Brasso and Cristol 2008), and as the breeding season progresses, their foraging activities become increasingly restricted to the area immediately surrounding their nests (Mengelkoch et al. 2004). Thus, tree swallows provide an excellent window into contaminant

availability at a highly localized scale. Additionally, tree swallows are unable to excavate their own cavities and so will readily adopt artificial nest boxes erected at sites of a researcher's choosing. Of further value is the fact that adults display a high degree of breeding site fidelity (Winkler et al. 2004), facilitating long-term studies of marked individuals. For these reasons, and many others, the tree swallow is quickly emerging as a model organism in ecotoxicology (McCarty 2002; Jones 2003).

### Study area

The South River, a tributary of the South Fork Shenandoah River in Virginia, USA, was contaminated with industrial mercury between 1929 and 1950 (Carter 1977). Cristol et al. (2008) documented significantly elevated mercury levels in the blood and feathers of nearly all songbird species breeding within 50 m of the contaminated river, including tree swallows. In 2005, a nest box trail was established at 19 contaminated sites along the South River as well as at 17 reference sites located upstream of the contamination source, and along the nearby North and Middle Rivers (centroid of study area: 38°10' N, 78°59' W; Fig. 1 in Cristol et al. 2008). Boxes were constructed following a popular bluebird nest box design (North American Bluebird Society 2009) and each was fitted with a "stovepipe" predator guard which reduced snake and mammalian predation (i.e. nest failure was <10% in 2005–2007). Boxes were placed approximately 25 m apart in cropland or pasture, within 50 m of river shoreline in 2005–2006, and up to 450 m into the floodplain thereafter. In 2005, 146 nest boxes were available. This number was increased to 296, 361, and 504 before the breeding seasons of 2006, 2007, and 2008, respectively. There is no natural wetland habitat suitable for tree swallow nesting in the study area, and prior to the establishment of our nest box trail, few, if any, tree swallows were nesting on or near any of our sites (D. A. Cristol, personal observation).

### Capture and sampling

During the breeding seasons of 2005–2008, we captured adult tree swallows in their nest boxes during incubation or the nestling period either by hand or using one of two trapping methods (Stutchbury and Robertson 1986; Friedman et al. 2008). Sex was determined by the presence of a brood patch in females or cloacal protuberance in males. Tree swallows are a rarity among birds in that females, but not males, exhibit delayed plumage maturation (Robertson et al. 1992). Thus, we were able to age adult females as either 'second-year' (hatched during the previous breeding season, hereafter 'SY') or 'after-second-year' (hereafter 'ASY') on

the basis of plumage. In contrast, all adult males have a similar plumage and were therefore classified as after-hatch-year (hereafter 'AHY'). Upon capture, individuals were banded with a unique USGS aluminum band. Additionally, a small blood sample ( $\sim 100 \mu\text{l}$ ) was collected from the brachial vein of each bird following the methods of Brasso and Cristol (2008).

### Mercury analysis

Mercury analysis was conducted at either the Trace Element Research Laboratory of Texas A&M University or at the College of William and Mary. Blood samples were analyzed for total mercury concentration on a Milestone® DMA-80 (see methods in Cristol et al. 2008). Approximately 95% of the mercury present in avian blood is in the organic form (Evers et al. 2005; Wada et al. 2009); thus, total mercury concentration should provide a reasonable approximation of methylmercury present in tissues. All mercury values are presented as wet/fresh weight ( $\mu\text{g/g}$ ) concentrations.

Quality control/quality assurance data are reported only for samples run at the College of William & Mary, as those for samples run at the Trace Element Research Laboratory, as well as an inter-lab comparison, have been reported elsewhere (Hawley et al. 2009). Every 20 samples included two samples of each of two standard reference materials (DORM-3, DOLT-3, or DOLT-4, National Research Council, Canada), a method blank, a sample blank, and a sample replicate (i.e., second capillary tube of blood from the same bird collected at the same time). Mean (weighted) percent recovery of the 3160 samples of standard reference materials used during the running of these samples was 98.96% (DORM-3 jar 1 = 100.75%, DORM-3 jar 2 = 98.79%, DOLT-3 = 98.71%, DOLT-4 = 98.94%). Relative percent difference between the duplicate samples was  $5 \pm 18\%$  ( $n = 199$  pairs of samples). Minimum detection limit ranged from 0.003 to 0.006  $\mu\text{g}$  during the period of analysis.

### Statistical analyses

We used Cormack-Jolly-Seber (CJS) models in Program MARK (White and Burnham 1999) to evaluate whether mercury exposure was associated with survival in adult tree swallows. CJS models are employed in studies involving live recaptures of marked individuals and can be used to estimate two parameters: apparent survival ( $\Phi$ )—the probability that an individual sampled at time  $t$  survives and returns to the study area at time  $t + 1$  (equal to one minus the probability of death or permanent emigration), and recapture rate ( $p$ )—the probability that an individual that is alive and present in the study area at time  $t$  is

actually detected during this same period. For each swallow banded during the course of the study, we created an encounter history consisting of a series of '1's and '0's, where a '1' signified that the individual was captured in a particular year, and a '0' signified that it was not. Thus, the encounter history '1010' would represent an adult bird that was captured in the first and third years of the study, but that remained undetected during the second and fourth years. As demonstrated in this example, detection is often imperfect. The usefulness of mark-recapture analysis lies in its ability to account for this imprecision by assessing how frequently individuals are, in effect, 'missed.' The end result is an estimate of apparent survival that is corrected for recapture rate.

We evaluated 11 a priori candidate models representing our hypotheses that sex, site type (contaminated or reference), and mercury exposure (individual cumulative blood mercury level) affected apparent survival and recapture of adult swallows across four annual sampling occasions (2005–2008).

First, we predicted that the effect of mercury on annual survival might vary according to sex. Sex differences in survivorship are common across many bird species, and likely reflect differences in life history (reviewed in Stutchbury et al. 2009). Given the unique set of stressors placed on each sex, we predicted that the additional impact of mercury on survival might differ between males and females.

We also evaluated whether exposure to elevated mercury may have influenced survival independent of dose. Such a relationship could be indicative of an 'all-or-nothing' response (Custer et al. 2007) or could reflect the potential for mercury to indirectly affect survival probability by altering large-scale components of the environment (e.g. food availability, see Gerrard and St. Louis 2001). To test for this relationship, we examined site type (contaminated or reference) as a variable in several models.

Finally, survival probability might covary with mercury exposure in a dose-dependent manner. To investigate this possibility, we created an index of individual exposure designed to reflect the potentially additive nature of mercury accumulation (e.g. Evers et al. 2008). Individual cumulative blood mercury level was calculated as the sum of all previous and current blood mercury levels recorded for each individual at a given point in time (i.e. 2007 cumulative Hg = 2005 Hg + 2006 Hg + 2007 Hg). When no mercury level was available, we either assigned a blood concentration that represented the average of all other years of exposure for that individual (for individuals captured multiple times,  $n = 18$ ), or we eliminated the individual from analysis (for individuals captured once,  $n = 11$ ). There was very little movement between contaminated and reference sites during the course of our study ( $n = 3$  birds,

all eliminated from analysis); therefore, we assumed that an individual's average mercury level would provide a reasonable measure of exposure in a single year. Survival was confirmed upon initial recapture in each year; we did not consider mercury levels in 2008, the final year of our study, as these were heavily influenced by mercury accumulated after the birds had successfully migrated back to the study site, and would not have influenced survival as determined at the beginning of that year.

We evaluated all additive (+) and two-way interaction (\*) models of sex, site type, and mercury exposure, and a null model where survival was held constant across all time intervals and groups. Because a greater emphasis was placed on capturing females in all four years of study, we allowed  $p$  to vary by sex in all 11 candidate models. Banded nestlings that returned to breed in our study area ( $n = 83$ ) were incorporated into the data set beginning in their first adult year.

We used numerical likelihood to estimate parameters and information theory to evaluate the relative support for each candidate model (Burnham and Anderson 2004). We assessed goodness-of-fit of the full model ( $\Phi_{\text{sex}+\text{site}+\text{time}+\text{sex}^*\text{site}+\text{sex}^*\text{time}+\text{site}^*\text{time}} p_{\text{sex}}$ ) with the median  $\hat{c}$  procedure. We used quasi Akaike's Information Criterion corrected for small sample size and overdispersion (QAIC<sub>c</sub>) and Akaike weights to assess the relative support in the data for each candidate model. The model with the lowest QAIC<sub>c</sub> score ( $\Delta \text{QAIC}_c = 0$ ) was considered the best fit to the observed data. Models with  $\Delta \text{QAIC}_c$  scores  $<2$  were considered well-supported and models with  $\Delta \text{QAIC}_c < 5$  were considered to be moderately supported. We report model-averaged estimates of apparent survival and recapture probability by year, sex, and site type. In addition, we report differences in apparent survival between reference and contaminated sites (effect sizes) with standard errors calculated using the Delta method.

## Results

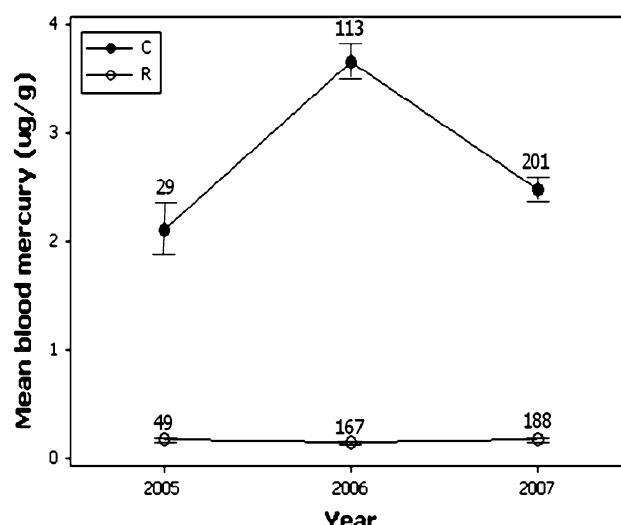
### Blood mercury levels

We used a general linear model to investigate three factors affecting blood mercury levels in tree swallows: year, site type, and sex (Table 1). Blood mercury levels differed by site type, and were, on average, an order of magnitude higher on contaminated than on reference sites (2005–2007 combined mean  $\pm$  SE: contaminated:  $2.84 \pm 0.09 \mu\text{g/g}$ , reference:  $0.17 \pm 0.01 \mu\text{g/g}$ ; Fig. 1). Annual variation on contaminated sites was considerable, while mercury levels on reference sites remained uniformly low throughout the duration of the study (Fig. 1). We observed no effect of sex

**Table 1** Summary statistics for general linear model investigating mercury accumulation in breeding adult Tree Swallows

| Factor         | df | F      | P      |
|----------------|----|--------|--------|
| Site type      | 1  | 577.16 | <0.001 |
| Sex            | 1  | 0.10   | 0.75   |
| Year           | 2  | 23.46  | <0.001 |
| Site type*sex  | 1  | 0.10   | 0.76   |
| Site type*year | 2  | 28.27  | <0.001 |
| Sex*year       | 2  | 0.23   | 0.79   |
| Error          |    | 737    |        |
| Total          |    | 746    |        |
| $R^2 = 60.7\%$ |    |        |        |

Individual blood mercury level was the response variable, while site type (contaminated or reference), sex (male or female), year (2005, 2006, or 2007), and all two-way interactions were included as fixed factors in the model



**Fig. 1** Mean ( $\pm$ SE) blood mercury in adult tree swallows breeding on either contaminated (C) or reference (R) sites in each of the first three years of the study (2005–2007). Sample sizes are represented as numbers above intervals

on exposure, indicating that males and females exhibited a similar tendency to accumulate mercury (Table 1).

### Adult survival

We obtained 1233 captures and recaptures, representing 932 individuals (444 from contaminated sites and 488 from reference sites; 130 recaptures on contaminated sites and 171 on reference sites). The full model ( $\Phi_{\text{sex}+\text{site}+\text{time}+\text{sex}^*\text{site}+\text{sex}^*\text{time}+\text{site}^*\text{time}} p_{\text{sex}}$ ) fit the data well (goodness-of-fit:  $P > 0.05$ ). We used the  $\hat{c}$  adjustment of 1.28 in our analysis to make the parameter estimates as robust and valid as possible.

**Table 2** Models of apparent survival ( $\Phi$ ) and recapture probability ( $p$ ) for adult tree swallows in Virginia

| Model # | Model <sup>a</sup>      | K <sup>b</sup> | $\Delta\text{QAIC}_c^{\text{c,d}}$ | w <sub>i</sub> <sup>e</sup> |
|---------|-------------------------|----------------|------------------------------------|-----------------------------|
| 1       | $\Phi \cdot p_s$        | 3              | 0.000                              | 0.252                       |
| 2       | $\Phi_s p_s$            | 4              | 0.887                              | 0.162                       |
| 3       | $\Phi_{Hg} p_s$         | 4              | 1.343                              | 0.129                       |
| 4       | $\Phi_{st} p_s$         | 4              | 1.392                              | 0.126                       |
| 5       | $\Phi_{s+Hg} p_s$       | 5              | 2.260                              | 0.081                       |
| 6       | $\Phi_{s+st} p_s$       | 5              | 2.355                              | 0.078                       |
| 7       | $\Phi_{st+Hg} p_s$      | 5              | 3.273                              | 0.049                       |
| 8       | $\Phi_{s+st+s*st} p_s$  | 6              | 3.796                              | 0.038                       |
| 9       | $\Phi_{s+Hg+s*Hg} p_s$  | 6              | 3.827                              | 0.037                       |
| 10      | $\Phi_{s+st+Hg} p_s$    | 6              | 4.225                              | 0.030                       |
| 11      | $\Phi_{st+Hg+s*Hg} p_s$ | 6              | 5.159                              | 0.019                       |

<sup>a</sup> Model structure:  $\Phi$  probability of apparent survival,  $p$  probability of recapture,  $\cdot$  time-constant survival,  $s$  sex,  $Hg$  cumulative mercury exposure,  $st$  site type (contaminated or reference). Recapture probability ( $p$ ) varied by sex in every model

<sup>b</sup> K = number of estimable parameters

<sup>c</sup> QAIC<sub>c</sub> = quasi Akaike Information Criterion corrected for small sample size

<sup>d</sup>  $\Delta\text{QAIC}_c$  = difference between QAIC<sub>c</sub> of the current model and the best supported model. Thus, the best supported model has  $\Delta\text{QAIC}_c = 0$

<sup>e</sup> w<sub>i</sub> = Relative likelihood of a model among the 11 tested

The model in which survival was constant across all groups and time intervals was the most parsimonious and had a 25% chance of being the best fit to the data (Table 2). Three univariate models in which survival varied according to sex, individual mercury exposure, and site type were also well-supported ( $\Delta\text{QAIC}_c$  scores <2; Table 2); several additive and interaction models received weaker support. Model-averaged estimates of apparent survival were higher for females than for males; female survival ranged from 0.473 to 0.488 and male survival ranged from 0.444 to 0.457 (Table 3). For both sexes, survival estimates varied

little from year to year. As expected, model-averaged recapture probability was greater for females ( $0.889 \pm 0.047$  SE) than for males ( $0.723 \pm 0.100$  SE), reflecting observed difference in ease of capture.

There is some evidence from the model selection analysis suggesting that individual mercury exposure and breeding site type were important for determining apparent survival; however, the effect is weak. Model-averaged survival probability for females and males breeding on reference sites was on average 1% ( $\pm 0.04$  SE) higher than for individuals breeding on contaminated sites (Table 3). The difference in survival probability between reference and contaminated sites increased to as high as 2% ( $\pm 0.05$  SE) when models that did not include either site type or individual mercury exposure (models #1 and #2, Table 2) were excluded from model averaging (i.e. estimates of apparent survival were computed by averaging over the remaining nine models; Table 3).

## Discussion

Adult tree swallows breeding at contaminated sites along the South River were exposed to significantly elevated levels of mercury. In fact, the levels of mercury observed in individuals at this site rank among the highest ever reported in a free-living songbird (Brasso and Cristol 2008). Our results indicate that some variation in annual adult survival for this species may be attributable to mercury exposure. Contaminated birds suffered a 1% reduction in survivorship compared with conspecifics breeding on reference sites. However, error surrounding this estimate is high, making biological interpretation difficult.

For any organism, survival necessarily represents the culmination of physiological stamina and endurance. Thus, any accumulation of stressors that undermine physiological performance could potentially hinder survival. Previous

**Table 3** Model-averaged estimates of apparent survival and standard errors for adult tree swallows breeding on reference ( $\Phi_R$ ) and contaminated ( $\Phi_C$ ) sites in 2005–2008

| Year <sup>a</sup> | Sex    | Reference |       | Contaminated |       | Full model set    |       | Reduced model set |       |
|-------------------|--------|-----------|-------|--------------|-------|-------------------|-------|-------------------|-------|
|                   |        | $\Phi_R$  | SE    | $\Phi_C$     | SE    | $\Phi_R - \Phi_C$ | SE    | $\Phi_R - \Phi_C$ | SE    |
| 2005              | Female | 0.488     | 0.035 | 0.477        | 0.041 | 0.011             | 0.035 | 0.020             | 0.044 |
| 2006              | Female | 0.486     | 0.036 | 0.475        | 0.039 | 0.011             | 0.036 | 0.018             | 0.045 |
| 2007              | Female | 0.483     | 0.046 | 0.473        | 0.038 | 0.010             | 0.046 | 0.017             | 0.059 |
| 2005              | Male   | 0.457     | 0.054 | 0.448        | 0.056 | 0.009             | 0.052 | 0.015             | 0.045 |
| 2006              | Male   | 0.455     | 0.054 | 0.447        | 0.055 | 0.008             | 0.029 | 0.014             | 0.046 |
| 2007              | Male   | 0.451     | 0.060 | 0.444        | 0.054 | 0.007             | 0.030 | 0.013             | 0.050 |

Differences in apparent survival were calculated based on model-averaged estimates from (1) all 11 models, and (2) a reduced set of nine models that excluded models that did not contain either an effect of site type or individual cumulative mercury exposure

<sup>a</sup> Refers to year t in survival interval from t to t + 1 (e.g. 2005 = interval from 2005–2006)

work on the South River has documented impairments in reproduction (Brasso and Cristol 2008), singing behavior (Hallinger et al. 2010), humoral immunocompetence (Hawley et al. 2009), and endocrine functioning (Wada et al. 2009) in contaminated songbirds. Given these findings, and the relatively high mercury levels at this site, it may seem surprising that contaminated swallows did not exhibit a more severe depression in annual survival.

One possible explanation is that a larger difference in survival may have existed, but been unintentionally obscured by limitations of our analysis. Mark-recapture analyses are notoriously data-intensive, and our study, involving 932 individuals followed over four sampling intervals, is relatively sparse when one considers that many comparable analyses involve thousands of birds sampled over several decades (e.g. Brown and Brown 2009). Small sample size and variation in responses of individuals to toxins can inflate error terms and reduce precision of survival estimates. Thus, statistical uncertainty may have hindered our ability to detect differences in survival.

It is also important to acknowledge the potential shortcomings of our index of individual cumulative mercury exposure. For this index, we assumed no mercury exposure prior to each individual's first capture. In the case of newly-caught SY females, this assumption should be valid, given that we can be sure that such females are in their first adult year (see Capture and Sampling). However, in the case of ASY females and all males, we cannot be similarly certain of past exposure history. Among newly-caught ASY females (of whose adult status in the previous year we can be sure), there is evidence to suggest that many spent a substantial portion of the prior breeding season as non-territorial floaters on the same sites on which they would later breed (Hallinger and Cristol 2010). Furthermore, floaters have been shown to accumulate levels of mercury comparable to those of resident breeders (Hallinger and Cristol 2010). Therefore, we very likely underestimated cumulative mercury exposure for many individuals on contaminated sites. Whether and how such bias could have influenced our results remains unclear. However, we performed a mark-recapture analysis involving only SY females (of whose exposure history we could be certain), and obtained parameter estimates very similar to those involving all birds (data not shown). Thus, it seems unlikely that this bias substantially impacted our results beyond adding unexplained variance.

Finally, it is possible that the 1% reduction in survival that we observed, although small, accurately reflects the impact of mercury on this important demographic rate. Although much progress has been made in identifying physiological and reproductive correlates of survival (e.g. Stearns 1992; Ardia et al. 2003; Ardia 2005), the complex interplay among many life history components

remains poorly understood. Thus, there may be real biological reasons why, for example, a reduction in immune system functioning (Hawley et al. 2009) is not reflected by a similar decrease in survival probability, and such findings underscore the need for further research into the physiological mechanisms governing survivorship.

Despite the vast literature detailing mercury exposure and effects on wildlife, few attempts have been made to measure the impact of mercury on avian survivorship (Seewagen 2010). To our knowledge, no study has yet been able to demonstrate an unambiguous link between contamination level and subsequent survival in free-living birds (see Thompson et al. 1991; Meyer et al. 1998; Ackerman et al. 2008; Mitro et al. 2008). This raises the interesting possibility that survival rates in general may be less sensitive to mercury exposure than a number of other commonly measured biological indices, such as reproductive success or immunocompetence. The reasons for this are not entirely clear, but several possibilities come to mind.

First, it may be a simple issue of scaling, whereby the factors governing lower levels of biological organization, such as intracellular processes, are more readily perturbed by short-term fluctuations in environmental conditions than are large-scale demographic processes such as survival. Essentially, this would amount to a "trickle up effect" of mercury, with disruption of many cellular and physiological systems being required before any impact on survival would become apparent.

Alternatively, it is possible that important effects on survival might manifest as changes in population structure and function rather than as differences in absolute survival probability. For example, selection pressures may vary as a result of mercury exposure, leading to differential survival of birds bearing different attributes than would be favored in uncontaminated areas; such differences may persist even though, in absolute terms, the number of birds surviving on each site is similar. Future work could benefit from considering the complex interactions between individual traits and survivorship of birds living in polluted areas.

Finally, it is important to note that the swallows in this study spent approximately five months at their contaminated or reference breeding sites and the rest of the year migrating or on their wintering grounds in Central America and southern North America. Judging from the low levels of mercury found in returning swallows on reference sites, there was little exposure to mercury when away from the breeding site. Additionally, because these swallows molt almost their entire plumage each fall (Robertson et al. 1992), and molt offers an opportunity to reduce load of mercury in vital tissues (Condon and Cristol 2009), it is possible that the effects of mercury on survival were blunted as a result of this annual recovery period. A similar

study on a non-migratory species might reveal a greater impact of mercury on survival.

In their study of common loons, Mitro et al. (2008) point out that even small decreases in survival rate (<3%) could have potentially serious consequences for viability of loon populations, members of which may live more than 30 years. In contrast, the average lifespan of tree swallows has been estimated to be 2.7 years (Robertson et al. 1992). Thus, it seems unlikely that the small depression in survival that we observed would disrupt population dynamics of this short-lived songbird. Even so, the results of our study may offer important insight into conservation of other bird species contending with mercury contamination, especially those exposed to elevated mercury year-round. Tree swallows are quickly becoming a model organism in many branches of ecology (Jones 2003), and are an excellent sentinel for investigating the effects of contaminants in free-living avian populations. However, at our study site, a number of songbird species, including several residents, have accumulated levels of mercury that equal or exceed those found in tree swallows (Cristol et al. 2008). Although tree swallows are not currently a species of conservation concern, it is our hope that this study will contribute to establishing a framework from which researchers can begin to understand the influence of mercury on complex demographic processes in a wide array of impacted wildlife.

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